Food Taste Chemistry

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FOREWORD

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PREFACE

The symposium on which this book is based was one of the few symposia, ever, totally devoted to the chemistry of food tastes. Most previous symposia have dealt with food flavors, where flavor is considered to consist mostly of odorous sensations.

Taste has long been considered to consist of only four sensations that contribute little to most food flavors. These four feeble sensations were linked to a simplistic taste chemistry that had little relevance to modern chemistry. These conceptions, often repeated, not only totally ignore the major role taste plays in food selection and the control of ingestion, but also are not followed in practice by much of the flavor industry. Thus you will often discover upon reading the literature that the "odors" of a food were best, or perhaps only, realized when food was in the mouth. Many flavor chemists have found that in order to adequately define a food flavor, tastes other than the four basics must be postulated. The types of taste active compounds in foods encompass much of natural product chemistry. Many of the compounds presently identified as odors are strongly taste active.

To help lay a new groundwork for the study of the tastes of foods, the speakers at the symposium presented papers on a variety of topics related to food taste chemistry. The problems in taste are of great complexity, involving biological as well as chemical variables. For a taste chemist, the types of sensations elicited and their measurement are as important as the nature of the compounds eliciting them. Various aspects of these problems are treated in detail in the papers in this volume.

The findings presented at this symposium have relevance far outside the narrow area of flavor chemistry. The taste measurements of the chemical properties of nutrient solutions have applications that range from physical organic chemistry to human nutrition.

Special thanks are due to the Japanese cochairman M. Namiki and the members of the Agricultural and Food Chemistry Division of ACS, especially G. Charalambous, R. Teranishi, and C. Mussinan for organizing and scheduling the symposium. I thank J. Oravec, Ng. Hoang, and the ACS Books Department for assistance in preparing this volume for publication.

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September 13, 1979

JAMES C. BOUDREAU

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Taste and the Taste of Foods

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In this paper the term taste will refer to all the chemical sensory systems of the oral cavity and their sensations. These sensory systems are intimately involved in the selection of food items and in the regulation of food intake. As we shall see, there are a variety of different taste systems attuned to different chemical aspects of food. These taste systems perform an exact and elaborate analysis of the chemical constituents in the food we eat.

The structure and function of these taste systems will be discussed in the context of a natural nutritional ecosystem, i.e. one in which man is not a disruptive element. Human taste systems are assumed to have developed to function in this natural system and to have changed little as a result of the cultural dietary changes that have occurred in the last 10- 20,000 years.

The natural nutritional ecosystem of man is assumed to be one in which both plant and animal foods are eaten (Figure 1) and they are eaten raw. In a natural nutritional ecosystem, taste serves a primary role in regulating the flow of compounds (1, 2). Certain things are to be eaten by us. Other things by others. There exists wide variation in the tastes of natural foods. Thus Cott has shown that certain birds and their eggs are both conspicuous and ill tasting (3, 4). The types of foods we consume now represent a selection from the vast array of items naturally available during our evolutionary development. The chicken egg for instance, represents a selection of one of the best tasting eggs naturally available (Figure 2).

We consume and transform plant and animal substances to promote certain physiological activities (the probable role of taste in mammalian sexual behavior is not considered here). Primary among these physiological functions is the replacement of body compounds and the supply of compounds for metabolic energy systems. Thus taste serves to regulate the consumption of needed compounds. Almost without exception, natural things that taste good are good for you and foods that are needed taste good even though your stomach is full. Toxic compounds almost

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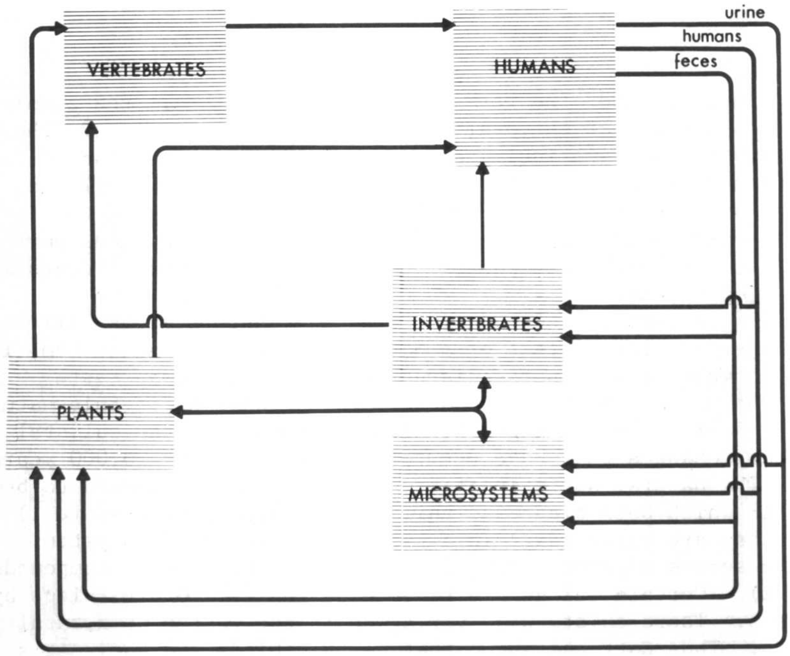
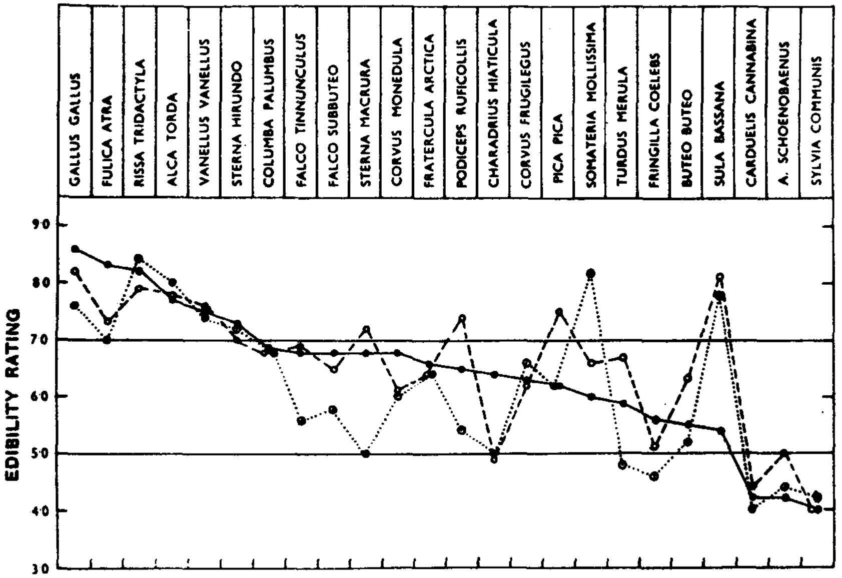


Figure 1. Flow diagram of the natural nutritional ecosystem of the human (simplified)



Proceedings of the Zoological Society of London

Figure 2. Preferences of man (●—●), rat (○ – – – ○), and hedgehog (○ · · · ○) for some eggs of different species of birds (4). *The species* Gallus gallus *is the chicken.*

invariably have noxious tastes. One exception (omitting marine substances) is the poisonous Amanita phaloides mushroom, a fungus that tastes good but will kill you. Not only do toxic foods have noxious tastes, but the thresholds for many toxic substances are extremely low. Another possible function of taste is the ingestion of compounds for the regulation of body temperature. Although there seems to exist little hard data on this matter, many human cultures classify foods into those that warm the body and those that cool it (5, 6). Taste may also function in the selection of pharmacologically active compounds for good health or good feeling. Things that taste good often make you feel good. In addition, many flavor compounds have antimicrobial actions and other pharmacological properties.

Anatomy of Taste Systems

A taste system can be considered to be composed of a receptor element for the transduction of chemical signals, a peripheral sensory neural system for the collection and transmission of chemical neural information, and a complex central nervous system for the analysis of this sensory neural information (7). The chemoreceptors that have been described in the oral cavity are of two basic morphological types: free nerve endings and taste buds. The so-called "free nerve endings" are distinguished on the basis of light microscopy as possessing no recognizable receptor or encapsulated ending. These free nerve endings are found throughout the oral cavity and are responsive to a variety of chemical compounds. A taste bud, on the other hand, is a receptor neural complex consisting of nerve fibers and 20-50 specialized cells organized in a fairly elaborate manner (Figure 3). The elongated taste bud cells are grouped together with one end forming the floor of the taste pit which opens up, through the taste pore, to the oral fluids. The taste bud cells project into the taste pore with either microvilli or an elongated bulb. The taste bud cells have been classified morphologically into three or more distinct types (8-12).

Taste buds, unlike free nerve endings, are not distributed throughout the oral cavity but rather are on the dorsum of the tongue, the soft palate, pharynx, epiglottis, larynx and upper third of the esophagus (Figure 3). On the tongue, taste buds are localized on protuberances known as papillae. The taste buds on the front two thirds of the tongue are located on the dorsal surface of the small fungiform papillae. At the rear of the tongue the taste buds are located in the foliate papillae and the vallate papillae. The posteriorly located chemosensory complexes contain large numbers of taste buds together with specialized secretory glands.

The peripheral sensory neurons that supply the chemoreceptors in the oral cavity reside in four distinct cranial ganglia (Figure 4). The trigeminal ganglion contains the sensory

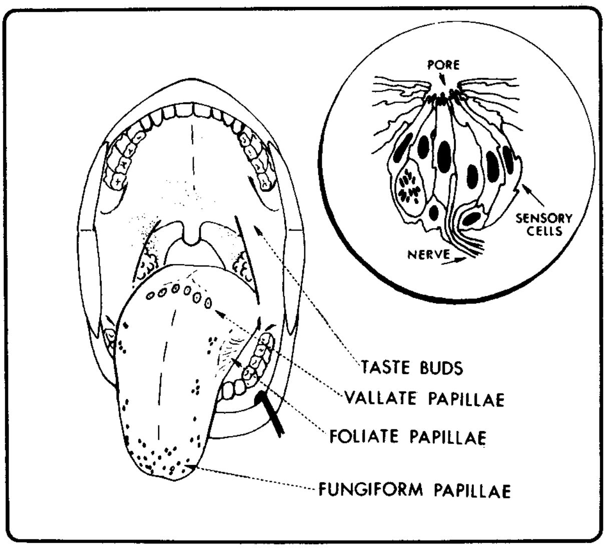


Figure 3. Location of some oral chemosensory receptor systems. Taste buds (schematic upper right) are found on specialized papillae on the tongue and scattered on the palate and posterior oral structures. Free nerve endings are found on all oral surfaces (94).

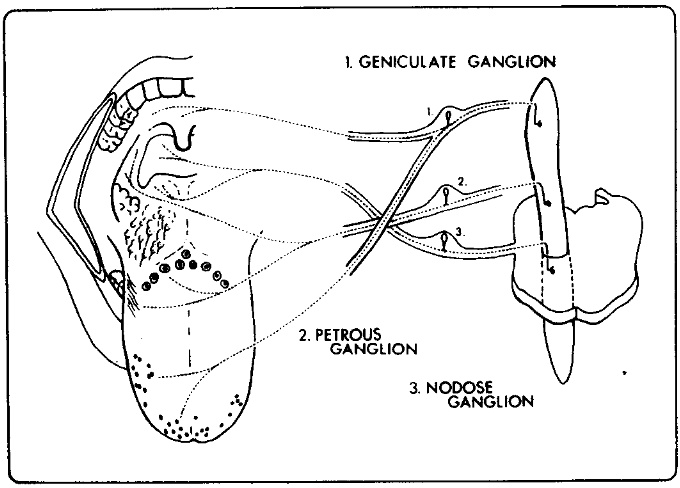


Figure 4. Peripheral sensory ganglia that supply nerve endings to taste buds in the mammalian oral cavity. Trigeminal ganglion, which supplies free nerve endings to all oral surfaces, not shown.

neurons providing free nerve endings to all parts of the oral cavity. The other three sensory ganglia innervate the taste buds, with each ganglion innervating buds on distinct locations. The taste buds on the fungiform papillae and the anterior soft palate are innervated by sensory neurons in the geniculate ganglion of the facial nerve. The taste buds on the foliate papillae, the circumvallate papillae, the posterior palate, the tonsils and the fauces are innervated by cells in the petrous ganglion of the glossopharyngeal nerve. Taste buds on the epiglottis, the larynx and the upper third of the esophagus are innervated by neurons in the nodose ganglion of the vagus nerve. Physiological and psychophysical studies on the functional properties of these different nerves and ganglia indicate that the chemosensory systems in the different ganglia are selectively responsive to different chemical aspects of foods.

Neurophysiology of Taste Systems

In examining the function of taste systems,various physiological measures are available to the investigator. Although, theoretically the neurophysiological responses of either the receptors or from any of the neurons in the sensorineural chain may be utilized, in practice, the most exact procedure is to measure the pulse trains being transmitted from the periphery to the central nervous system (Figure 5). Receptor potentials are subject to several sources of error, at least as regards quantitative measures of neural responses. For the precise study of neural responses to chemical stimulation the neural pulse is the measure of choice in sensory neurophysiology. These pulses are preferably measured from peripheral sensory neurons since neural interaction is minimized. Pulses may be measured from either the peripheral fibers of the sensory ganglion cells or from the somas. One advantage in recording pulses from the cells themselves is that small fiber systems are sampled, while there is a strong bias toward large fiber potentials in fiber recordings. The only ganglion cell system that has been examined in any detail is the geniculate ganglion system which innervates receptors on the fungiform papillae. The properties of these neurons will be reviewed for the cat, dog, and goat.

Typically, a geniculate ganglion cell innervates receptors on more than one fungiform papilla (Figure 5). The number of fungiform papillae innervated by a single neuron ranges from one to as many as twelve. Within a taste bud, a nerve fiber will contact many receptor cells. Almost all geniculate ganglion neurons exhibit pulse activity in the absence of experimenter designed stimulation (Figure 6). This "spontaneous activity" is usually of a complex irregular type that is characteristic of chemical sensory systems. Pulses are often emitted in bursts with fixed interspike intervals, with the burst interval

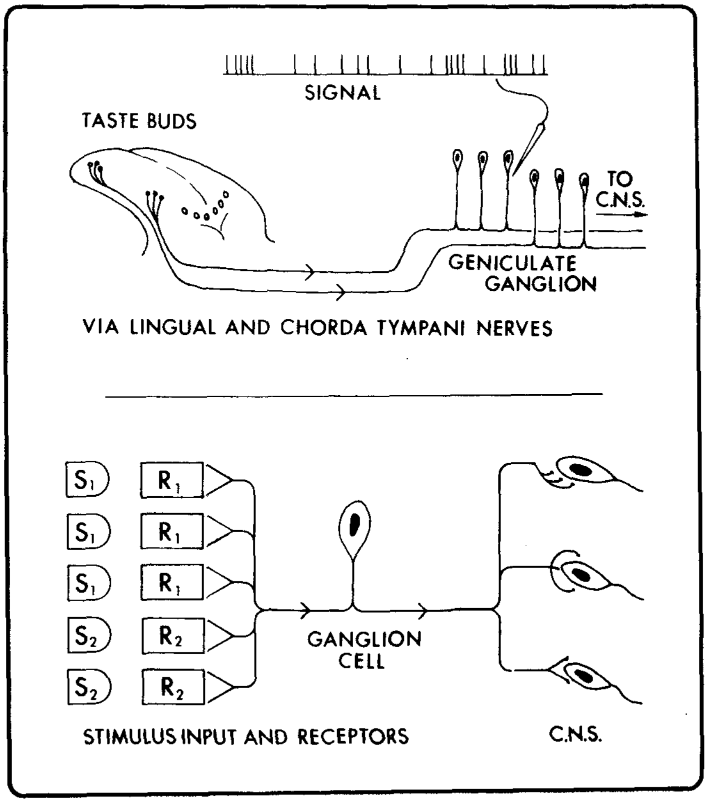


Figure 5. (lower) *Diagram of the peripheral and central connections of a sensory ganglion cell innervating the taste buds of the tongue.* (upper) *Illustration of the connections of sensory ganglion cells and the pulse signals used to encode sensory information.*

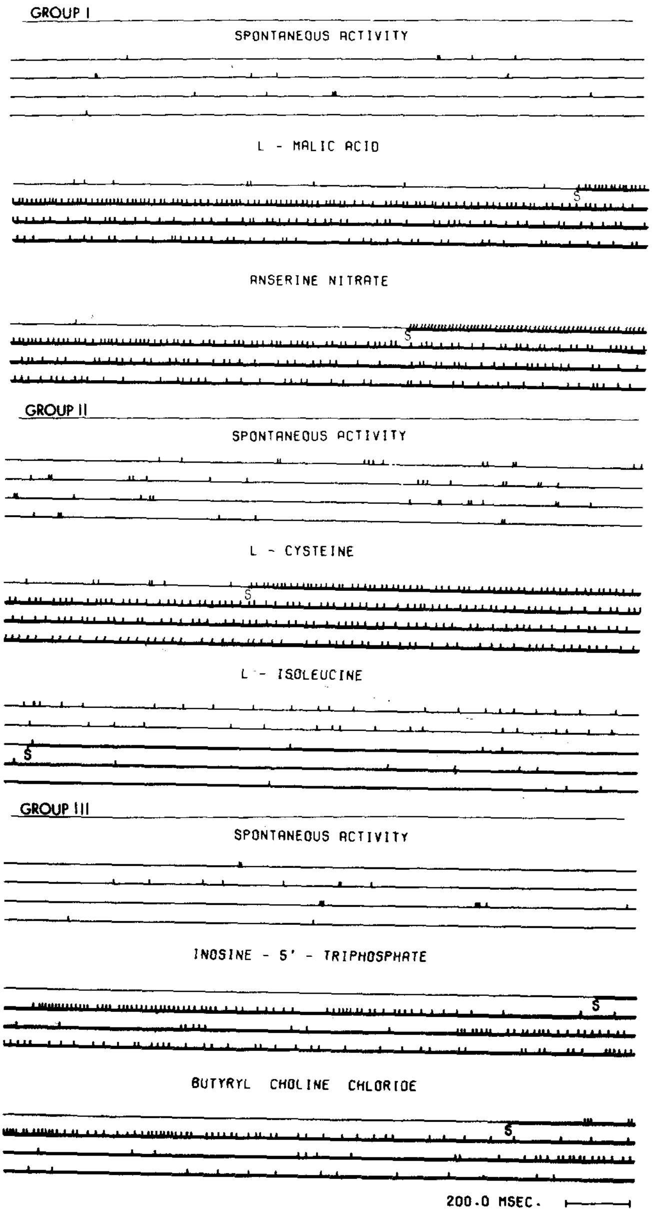


Figure 6. Spontaneous and evoked spike activity recorded from taste neurons of the geniculate ganglion of the cat. The classification of the three different sensory neurons is indicated by Groups I, II, and III.

decreasing as function of interval order.

This spontaneous activity may be inhibited by the application of a chemical solution to the tongue, or the neuron may be excited by a different solution. Mixing an inhibitory compound into an excitatory solution may result in an inhibitory solution. The neuron may be excited or inhibited by chemical stimulation of a single papilla in its papillae system (13), and excitation of two papillae simultaneously may result in an increase in discharge, with the increase being usually less than algebraic. The discharge resulting from the excitation of the neuron by stimulation of one papilla may be inhibited by the simultaneous stimulation of another papilla with an inhibitory solution.

Neurons of the geniculate ganglion have been found to be of more than one type when examined in terms of various physiological measures such as spontaneous activity rate and type, latency of spike discharge to electrical stimulation (a measure of conduction velocity and thus fiber size), and types of compounds activating. Neurons in both the cat and the dog can be classified into at least three different groups (10). Neurons in the goat have also been tenatively divided into three different groups, although only one of these groups is comparable to those in the two carnivores. The neural groups in the cat, goat, and dog tend to preferentially innervate fungiform papillae on somewhat different parts of the tongue (Figure 7), although there is extensive overlap, especially in the dog.

The determination of the types of compounds stimulating geniculate ganglion neurons constitutes an extensive field of continuing investigation. Not surprisingly, it has been found that many of the neurons are sensitive to solutions of foods commonly present in the animal's environment. Thus a goat neuron may respond to a carrot or herb solution and a cat to chicken or liver. Cats and dogs have been found to be highly responsive to many of the compounds found in meats, such as amino acids, the dipeptides, anserine and carnosine, and nucleotides. The goat has been less well investigated, but seems highly responsive to salts and alkaloids. Especially prominent in the stimulation of the carnivore are nitrogen and sulfur compounds, especially five and six member ring heterocycles. The different neural groups tend to be differentially responsive to chemical stimuli, illustrating their selectivity in the measurement of food compounds (Figure 8). Some of the similarities and differences among the geniculate ganglion neural groups of the cat, dog, and goat are summarized in Table I. As evident in this table, the dog geniculate ganglion systems are quite similar to the cat. One major distinction is that the dog amino acid sensitive neurons (class A units), although highly similar to cat group II units, are also responsive to sugar as well as the most stimulating amino acids and di- and tri- phosphate nucleotide salts. The goat neural groups on the other hand seem quite distinct from carnivoral taste systems with only the acid responsive group

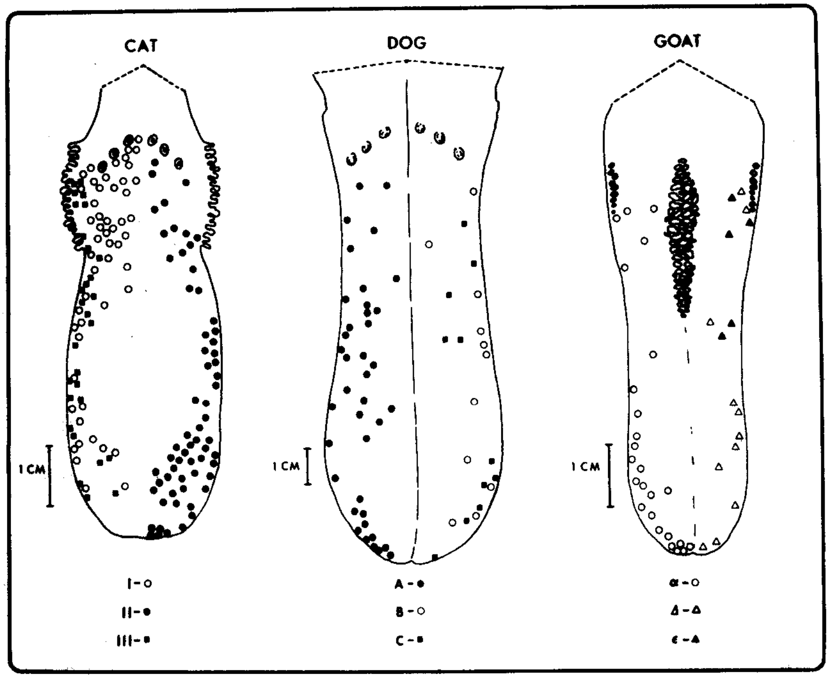


Figure 7. Peripheral innervation of fungiform chemoreceptors by neurons of the geniculate ganglion of three different species. In each species the neurons have been separated into three distinct neural groups (see Table I for comparison of chemical stimuli for the different neural groups).